Feeding behavior of newly settled winter flounder (*Pseudopleuronectes americanus*) on calanoid copepods

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Abstract

Field and laboratory investigations were conducted to examine feeding by newly settled winter flounder (*Pseudopleuronectes americanus*) on two co-occurring calanoid copepods, *Eurytemora affinis* and *Acartia hudsonica*. During the spring, these prey are present when winter flounder initiate their demersal lifestyle in estuaries of the northeastern United States. Epibenthic zooplankton were collected concurrently with winter flounder in the Navesink River estuary, NJ, in May 1998 and 1999. Although both calanoid species were in the estuary during the 2-year survey, *E. affinis* was consumed nearly to the exclusion of *A. hudsonica* by newly settled winter flounder. Annually, *E. affinis* and *A. hudsonica* had similar size distributions in field collections, indicating that species choice was not size selective. However, when preying on *E. affinis*, winter flounder preferred the larger sized organisms. In single species laboratory experiments, *E. affinis* and *A. hudsonica* were consumed equally by newly settled winter flounder (19–23 mm TL), but there were more strikes made toward *E. affinis*. Despite the lower catch efficiency, *E. affinis* was selected over *A. hudsonica* when the prey species were offered together in equal numbers. The selection for *E. affinis* over *A. hudsonica* by newly settled winter flounder may be the result of behavioral and/or morphological differences in the prey species. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Acartia hudsonica; *Eurytemora affinis*; *Pseudopleuronectes americanus*; Selective predation

1. Introduction

The winter flounder (*Pseudopleuronectes americanus*) is a commercially important flatfish which utilizes estuaries in the northeastern United States and Canada as spawning sites in winter through spring and as nursery habitat during the spring and summer (Able and Fahay, 1998). Little information exists on their diet and feeding behavior during the early post-settlement stage when growth is critical to survival. Pearcy (1962) and Stehlik and Meise (2000) found calanoid copepods to be primary prey items, however, both studies revealed an apparent specificity in the calanoid copepods consumed. Given the dynamic and relatively diverse spring copepod community in northeastern United States estuaries (Deevey, 1956; Jeffries, 1959; Cronin et al., 1962; Yamazi, 1966; Stepien et al., 1981), further research on predator–prey interactions between newly settled winter flounder and calanoid copepods was warranted.

There is increasing evidence that young fish feed selectively on zooplankton. Larval Atlantic herring (*Clupea harengus*), gulf menhaden (*Brevoortia patronus*), Atlantic mackerel (*Scomber scombrus*) and American sand lance (*Ammodytes americanus*) feed selectively on the copepodites of *Pseudocalanus* sp. over *Acartia* sp., tintinnids over copepod nauplii, the calanoid nauplii of *Temora longicornis* and *Pseudocalanus* sp. over *A. hudsonica*, and nauplii of *T. longicornis* over *A. hudsonica*, respectively (Checkley, 1982; Peterson and Ausubel, 1984; Stoecker and Govoni, 1984; Monteleone and Peterson, 1986). Yellow-eye mullet (*Aldrichetta forsteri*) and hardyhead (*Atherinosoma* sp.) consume the calanoid copepod *Paracalanus indicus* over *A. tranteri* (Kimmerer and McKinnon, 1989). A similar trend is seen in adult herring and sprat (*Sprattus sprattus*) which feed on the calanoid copepod *Eurytemora affinis* over *Acartia* spp. (Sandstrom, 1980; Hansson et al., 1990; Rudstam et al., 1992).

Stehlik and Meise (2000) speculated that newly settled winter flounder might feed selectively on calanoid copepods. During a long-term synoptic trawl survey of demersal fishes in the Navesink River estuarine system, NJ, only *E. affinis* was observed in over 200 winter flounder stomachs examined from a May 1997 survey. Yet, *Acartia hudsonica*, as well as *E. affinis*, can dominate this system during the spring (Sage and Herman, 1972; Shaheen and Steimle, 1995) when the young winter flounder are abundant. The ubiquity of *E. affinis* in the stomachs, as well as their historical co-occurrence with *A. hudsonica* in the system, suggested that *E. affinis* was the preferred prey of newly settled winter flounder.

In this study, we collected zooplankton concurrently with newly settled winter flounder to determine if in situ preferences for prey species, prey size or prey sex were exhibited by these young fish. We also conducted laboratory experiments to determine mechanisms of prey choice observed in the field. Newly settled winter flounder were fed monocultures of *E. affinis* or *A. hudsonica* to test whether consumptive rates were equivalent. These experiments were videotaped to qualify predator–prey behavior and quantify predator attacks. Other experiments were designed to test whether newly settled winter flounder consumed *E. affinis* and *A. hudsonica* in proportion to their initial concentrations.

2. Materials and methods

2.1. Study site

The Navesink River, located in central New Jersey, is a small flood-dominated riverine estuary known to serve as a spawning (Stoner et al., 1999) and nursery site (Phelan et al., 2000; Stoner et al., 2000) for winter flounder. It is approximately 9 km long with maximum depths near 3.0 m (MLW). The mean tidal range is ∼1.4 m and currents in channels can attain velocities of ∼1 m s^{-1} (Chant and Stoner, 2000). The Navesink River joins with the Shrewsbury River and empties into Sandy Hook Bay, which is located at the apex of the mid-Atlantic Bight (Fig. 1).

2.2. Field collections of zooplankton and winter flounder

Zooplankton were sampled at 12 stations (depth range: ∼0.5–2.5 m) in the river during May 1998 and 1999 (Fig. 1). Stations were shifted for broader coverage in 1999. The specific locations were chosen because they consistently yield the highest concentrations of early juvenile winter flounder (NMFS, unpublished data).

Zooplankton were collected during daylight hours with a 153 μm mesh conical net (0.25 m mouth diam. × 0.75 m length) fitted with a General Oceanics, Inc. standard
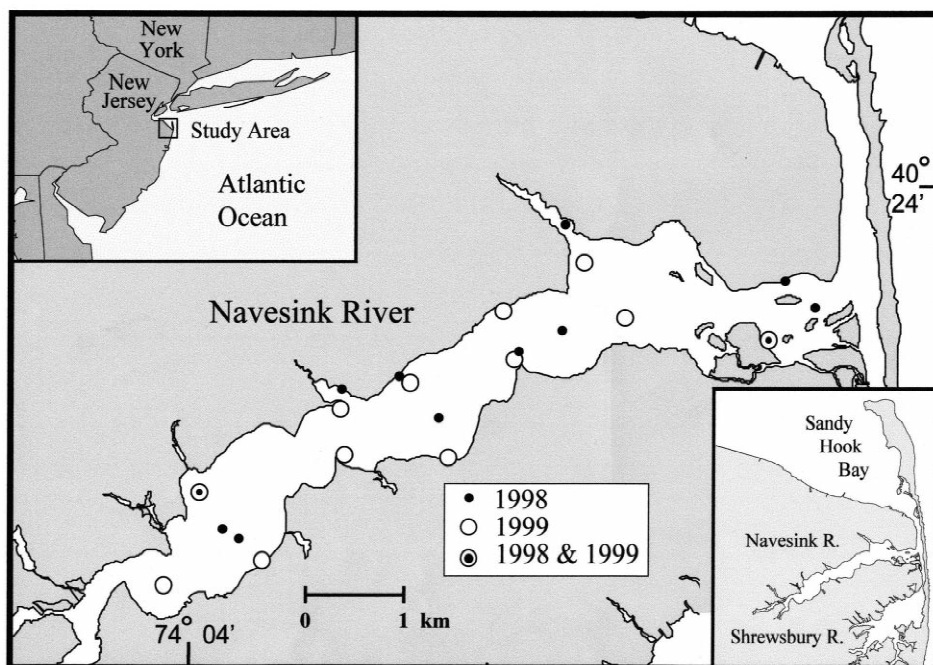

Fig. 1. The Navesink River, NJ. Stations sampled for zooplankton in May 1998 and 1999 are marked. Inset maps show general location and adjacent waterways.

flowmeter (model 2030R). A choke collar allowed deployment and retrieval in the closed position. The net was lowered on a towline equipped with a depressor, which allowed the net to fish 0.2 m above the bottom. The daylight near-bottom collections provided zooplankton available to the demersal winter flounder, which feed by day (MacPhee, 1978). Replicate tows ($n = 2$) at ~1 m s^{-1} for 60 s were made at each station. Zooplankton were preserved in the field with 5% buffered formaldehyde and returned to the laboratory for identification and processing.

Calanoid copepods available to the winter flounder were determined through analyses of density, size and sex of E. affinis and A. hudsonica from the field collections. Density was estimated by subsampling the collections with a 1 ml Henson–Stemple pipette until at least 400 organisms or 150 of the dominant species were counted (Lee and McAlice, 1979). The size distributions of prey species were assessed by measuring the carapace width (CW) (Blaxter, 1969; Ghan and Sprules, 1993) of a random sample of at least 20 individuals of each prey species from eight stations in 1998 ($n = 366$) and 12 stations in 1999 ($n = 498$) with an ocular micrometer. Also, in 1999 the male:female ratio of E. affinis was determined and 100 individuals of each sex were measured.

Newly settled winter flounder for our analyses were collected during the synoptic beam trawl survey in the Navesink River in 1998 and 1999 (unpublished data). Collections were made during daylight hours with replicate tows ($n = 2$) of a 1 m beam trawl (3 mm mesh) and 5 m otter trawl (6 mm mesh cod-end liner). For stomach content analyses, winter flounder were grouped into 10 mm size classes: 10–19, 20–29 and 30–39 mm TL. Calanoid prey in all stomachs were identified to species, counted, measured for CW (252 individuals from 15 fish in 1998 and 1114 individuals from 87 fish in 1999) and sexed (397 individuals from 50 fish in 1999).

2.3. Statistical analyses

Annual spatial patterns in the abundance of E. affinis and A. hudsonica at stations throughout the river were evaluated with a Kruskal–Wallis test. Two sample Kol-mogorov–Smirnov (KS) tests were used to test for differences in the (1) inter-annual size distribution of each prey species, (2) annual size distribution between prey species, (3) size distribution of calanoids from the field and in winter flounder stomachs, and (4) size distribution of prey consumed by the three size classes of fish. For these analyses calanoids were divided into four CW classes (< 0.14, 0.14–0.19, 0.20–0.25 and > 0.25 mm) (range 0.10–0.37 mm). Sex ratios of E. affinis in the field and diets of young fish were compared to determine whether fish selected prey of a specific sex. Male and female prey were pooled by tow for each size class of fish. A two-tailed t-test was used to compare the (1) widths of field-collected male and female E. affinis and (2) number of calanoid prey consumed by each size class of fish. For all analyses, only fish that had consumed at least three calanoid copepods were considered.

2.4. Laboratory feeding experiments

2.4.1. Collection and maintenance of experimental animals

All animals for the experiments were collected from Sandy Hook Bay in May 1999

and kept in aquaria with a continuous flow of ambient seawater at the James J. Howard Marine Sciences Laboratory (temperature = 14.6–17.2°C; salinity = 24.4–25.5‰). Newly settled winter flounder were collected within 7 days of the experiments with seines and maintained on *Artemia* nauplii fed ad libitum. Calanoid copepods were collected with a 363 μm mesh, 30 cm diameter conical net, 1 day before the start of experiments. They were transferred to holding containers in the aquaria and maintained on natural phytoplankton.

2.4.2. Experimental design

Newly settled winter flounder were offered three different prey treatments: (a) 100% *E. affinis* (seven replicates), (b) 100% *A. hudsonica* (seven replicates), and (c) 50% *E. affinis* and *A. hudsonica* (12 replicates). Treatments with 100% *E. affinis* and 100% *A. hudsonica* were videotaped.

Experiments were conducted in a temperature controlled room set at 15°C (close to ambient water temperature), with a 14:10-h light/dark cycle (day = 0600–2000 EST) and daytime illumination of 10–12 μE m^{-2} s^{-1}. Experimental chambers were clear acrylic cylinders (9 cm diam. × 11 cm high), with sand substrata (0.5 mm) and black paper taped to the outside. Experiments were videotaped from the side through a small aperture with a camera head fitted with a macrolens.

Newly settled winter flounder (19–23 mm TL) were transferred to individual containers without food 24 h before the experiments for acclimation and to standardize feeding motivation. Just prior to experiments, zooplankton samples were lightly anesthetized with MS222 and *E. affinis* and *A. hudsonica* were extracted and sorted (Preliminary tests showed that 98% of the copepods survived such handling and there were no apparent behavioral effects). No females with eggs or copepodid I–IV stages were chosen. A random sample of 25 individuals was measured for each species. Modal CW was 0.3 mm for both species and ranged from 0.2 to 0.4 mm for *E. affinis* and 0.2 to 0.3 mm for *A. hudsonica*. The prey were held in vials in the temperature controlled room and provided with a 1 h recovery period before being gently introduced into the containers with newly settled winter flounder.

Flounder were provided with a total of 50 copepods in each treatment, i.e. 50 of either *E. affinis* or *A. hudsonica* in the 100% treatments and 25 of each prey species in the 50% treatments. The fish were allowed to feed for 1 h, sacrificed for stomach analyses and the consumed organisms were identified and counted. All experiments were conducted between 1000 and 1400 h.

Videotapes from all of the 100% treatments were analyzed to ascertain the time required for initiation of foraging, predator–prey positions and activity during the experiments and the number of predator attacks on prey. An attack was recorded if the newly settled winter flounder oriented toward and lunged at a copepod. Subsequent attacks on the same prey item were counted but did not require repetition of the initial movements.

2.4.3. Statistical analyses

A one-tailed *t*-test was used to determine if differences in the mean number of prey consumed, predator attacks and percentage of successful attacks (attack success = prey

consumed/no. attacks $\times$ 100) occurred when newly settled winter flounder were fed either *E. affinis* or *A. hudsonica* (100% treatments).

A one-tailed *t*-test was also used to evaluate if newly settled winter flounder consumed different numbers of *E. affinis* and *A. hudsonica* in the 50% treatments. Further, Chesson's selectivity index (α, for cases without food depletion) (Chesson, 1983) was calculated for each fish. Chesson's α relates the proportion of food organisms in the environment to that consumed. Its value ranges from 0 to 1 and is an indicator of selective feeding behavior. (Random feeding is denoted by $1/n$, where $n =$ the number of species available. Values below and above $1/n$ suggest negative and positive selection, respectively.) The mean Chesson's α was compared in a one-sample one-tailed *t*-test to the expected mean with two prey species (0.5).

3. Results

3.1. Field surveys

Eurytemora affinis and *A. hudsonica* were present in the Navesink River in May 1998 and 1999 (Fig. 2) and dominated the zooplankton community. There was inter-annual variation in their relative abundance: in 1998, *E. affinis* was dominant with a mean density of $\sim$ 11 000 m^{-3}, while *A. hudsonica* was more abundant in 1999 with a mean density of $\sim$ 27 000 m^{-3}. A Kruskal–Wallis test showed no significant difference among stations in the abundance of *E. affinis* or *A. hudsonica* throughout the river in either year ($P > 0.05$).
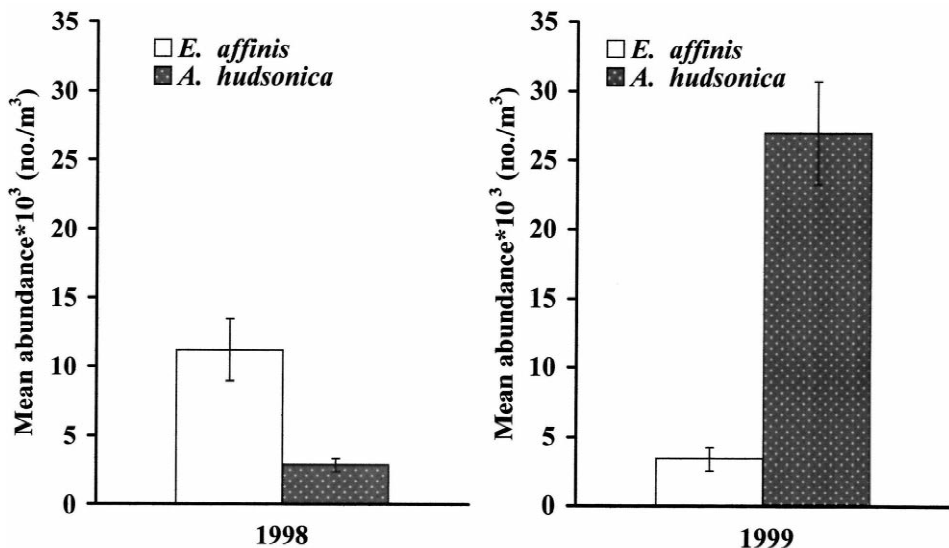

Fig. 2. Mean abundance of *E. affinis* and *A. hudsonica* in May 1998 and 1999 ($n = 12$) in the Navesink River, NJ (error bars $= \pm 1$ S.E.).

The two prey species had similar patterns in their size distributions during the 2-year survey (Fig. 3), but KS tests showed that significant differences existed. There was a significant difference in the size distribution between years for each species (KS: *E. affinis*, $P < 0.001$; *A. hudsonica*, $P < 0.001$) because higher percentages of small calanoids (< 0.14 and 0.14–0.19 mm CW) were collected in 1998. During both years, the size distribution differed between species (KS: 1998, $P < 0.01$; 1999, $P < 0.001$): there was always a lower percentage of *E. affinis* < 0.14 mm CW and a higher percentage 0.14–0.19 mm CW than *A. hudsonica*. The percentages of each population 0.20–0.25 and > 0.25 mm CW, however, were relatively consistent (Fig. 3).

Relatively few *E. affinis* females were collected in 1999, comprising just 15% ($\pm 31.5\%$) of the adult population. Females were also significantly larger than males (*t*-test: $t = 25.982$, df $= 199$, $P \leq 0.001$). The mean female CW was 0.32 mm (± 0.022), while males had a mean CW of 0.24 mm (± 0.021).

Despite the abundance of both copepods in the Navesink River, *E. affinis* was
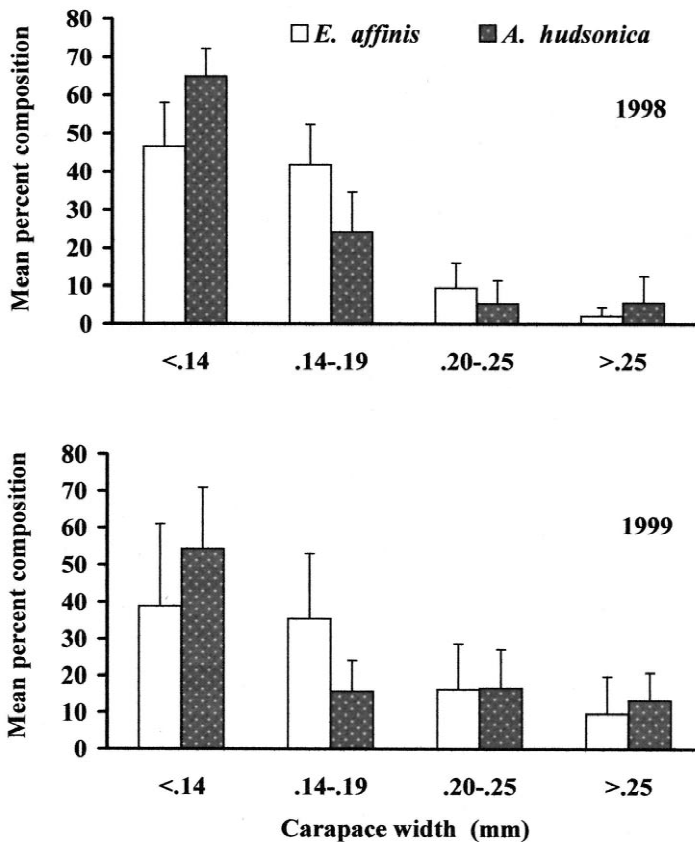

Fig. 3. Mean size distribution of *E. affinis* and *A. hudsonica* in May 1998 and 1999 in the Navesink River, NJ (error bars $= \pm 1$ S.D.).

Table 1

Number of *E. affinis*, percentage of each size class of *E. affinis* and percentage of male and female *E. affinis* consumed by newly settled winter flounder in the Navesink River, NJ, May 1998 and 1999[a]

Flounder size class (mm TL)	Total copepods consumed (n) 1998–1999	Copepod sizes consumed								Copepod sex consumed	
		1998				1999				1999	
		(n) <0.14	0.14–0.19	0.20–0.25	>0.25	(n) <0.14	0.14–0.19	0.20–0.25	>0.25	(n) Male	Female
10–19	12±1.5 (31)	(3) 7.7	38.5	46.1	7.7	(28) 5.5	14.6	47.7	32.2	(6) 46±21	54
20–29	45±4.9 (49)	(5) 25.0	35.7	25.0	14.3	(44) 2.7	15.3	32.7	49.3	(11) 21±20	79
30–43	52±12.6 (22)	(7) 21.3	27.7	23.9	27.1	(15) 2.0	7.8	27.2	63.0	(7) 23±15	77

[a] (n) = number of fish (fish from each size class were pooled by tow for male–female data in 1999); values are means±1 S.E. for total copepods consumed and means±1 S.D. for percentage of copepod gender consumed; no error is shown for copepod sizes consumed because values were derived from the KS analyses.

consumed to the near exclusion of *A. hudsonica* by winter flounder collected during both 1998 and 1999 surveys. In 1998, *E. affinis* was the only calanoid found in the stomachs of 15 winter flounder (18–32 mm TL). In 1999, all 87 winter flounder (13–43 mm TL) examined contained *E. affinis*, but two also contained *A. hudsonica* (one in each fish).

Eurytemora affinis was the dominant prey species in newly settled fish and consumed in large amounts (Table 1). The number of *E. affinis* eaten increased with predator size. On average, 12 *E. affinis* were found in fish 13–19 mm TL (max = 32) while 45–52 *E. affinis* were found in the larger size classes (max = 280). Winter flounder 20–29 and 30–43 mm TL showed no significant difference in the number of prey consumed (*t*-test: $t = -0.575$, df = 69, $P = 0.57$).

The size distribution of *E. affinis* consumed by all fish size classes was significantly different from the size distribution of prey in the field during each of the two surveys (KS: 1998, 10–19 mm TL ($n = 3$), $P < 0.01$; 20–29 ($n = 5$) and 30–43 ($n = 7$) mm TL fish, $P < 0.001$; 1999, 10–19 ($n = 28$), 20–29 ($n = 44$) and 30–43 ($n = 15$) mm TL fish, $P < 0.001$) (Fig. 4). A strong selection for the larger size classes of *E. affinis* (0.20–0.25 and > 0.25 mm CW) was exhibited by all size classes of winter flounder.

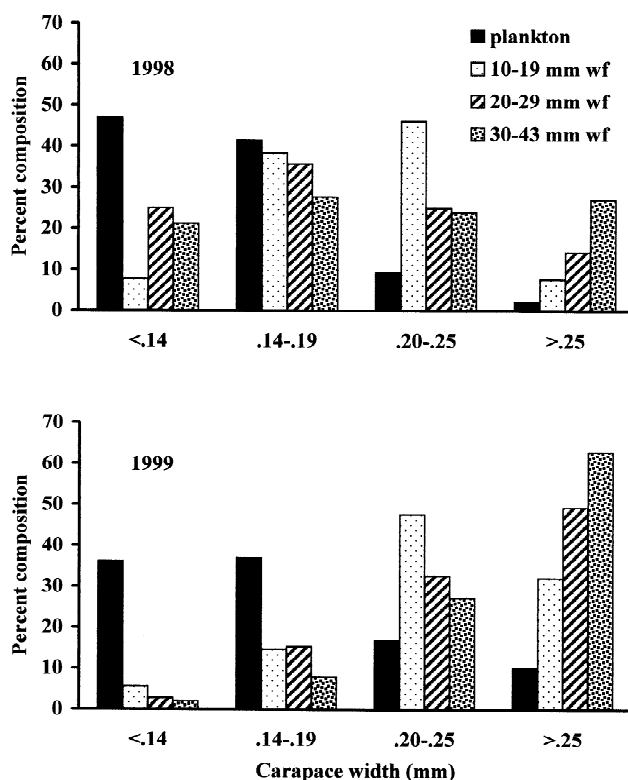Significant differences were observed in the size distribution of prey consumed among

Fig. 4. Size distribution of *E. affinis* in the plankton and consumed by winter flounder (wf) in May 1998 and 1999 in the Navesink River, NJ.

the three size classes of fish, in 1999 (KS: 10–19 vs. 20–29 mm TL, $P < 0.001$; 10–19 vs. 30–43 mm TL, $P < 0.001$; 20–29 vs. 30–43 mm TL, $P < 0.01$) (Table 1). Higher percentages of large prey in larger fish (20–43 mm TL) were responsible for this. The same trend was observed in 1998 but was not significant, probably because large *E. affinis* were relatively scarce or because the sample size ($n = 15$) was small. The size of *E. affinis* consumed by winter flounder increased with predator size: the largest *E. affinis* (> 0.25 mm CW) was consumed in the highest percentage by the largest fish (30–43 mm TL).

More female *E. affinis* than males (a ratio of 75:25) were consumed by the larger sized winter flounder (20–43 mm TL) (Table 1). In contrast, the ratio of female to male *E. affinis* in small fish (10–19 mm TL) was about 50:50.

3.2. Laboratory experiments

We examined predator–prey interactions from videotape analyses of the 100% treatments. Immediately after the introduction of copepods into the experimental containers, the newly settled winter flounder buried. On average, 4 min elapsed before re-emergence of the fish and initiation of foraging. By that time, the calanoids were just off bottom, sinking and rising or hovering. However, *E. affinis* movement was much quicker and more erratic than that of *A. hudsonica*, which was more slow and rhythmic. Neither predator nor prey appeared agitated during the experiments.

In single-prey laboratory experiments, the numbers of *E. affinis* (9) and *A. hudsonica* (11) consumed by newly settled winter flounder were similar, however, videotape analyses showed that significantly more attacks were made against *E. affinis* than *A. hudsonica* (28 vs. 19) (Table 2). With both copepod species, fish tracked the prey visually, paused, arched the caudal portion of their bodies upward, and struck. If the prey was missed, it was pursued and the strike was repeated. Young fish were significantly less successful in capturing *E. affinis* than *A. hudsonica* with success rates of 35 and 62%, respectively (Table 2).

In the 50% treatments, *E. affinis* was preferred over *A. hudsonica* by newly settled winter flounder. The average number of *E. affinis* consumed (6 ± 2) was significantly higher than that of *A. hudsonica* (3 ± 1) (one-tailed *t*-test: $t = -1.664$, df $= 10$, $P = 0.06$). A one-sample *t*-test ($H_o = 0.5$) on the mean Chesson's α showed a significant positive selection for *E. affinis* over *A. hudsonica* (Table 3).

Table 2

Behavior of newly settled winter flounder in 100% laboratory feeding experiments (50 *E. affinis* or 50 *A. hudsonica*)[a]

	No. consumed	No. attacks	Percent success
E. affinis	9±1	28±2	35±11.8
A. hudsonica	11±4	19±5	62±19.1
t	0.546	−1.714	2.267
P	0.30	0.06	0.015

[a] Values for no. consumed and no. attacks are means±1 S.E. Values for percent success are means±1 S.D. Probabilities were derived with a one-tailed *t*-test ($n = 5$, df $= 8$).

Table 3
Chesson's selectivity index (α) for newly settled winter flounder feeding on equal numbers of *E. affinis* ($n = 25$) and *A. hudsonica* ($n = 25$)[a]

Treatment	α	Expected α	t	P
E. affinis	0.68 ± 0.11	0.50	-4.068	0.01
A. hudsonica	0.32 ± 0.11	0.50	-4.068	0.01

[a] Values for α are means ± 1 S.E. ($n = 6$). A one-sample *t*-test (df = 10, one-tailed) compared mean α with expected α.

4. Discussion

Our field studies showed that *E. affinis* was the dominant prey species for newly settled winter flounder in the Navesink River, NJ, and was preferred even when the alternative prey species, *A. hudsonica*, was more abundant in near-bottom water. *Eurytemora affinis* also was preferred ($P < 0.01$) when offered with equal numbers of *A. hudsonica* in the laboratory. Previous descriptive studies have reported *E. affinis* as an important food for young winter flounder (Pearcy, 1962; Stehlik and Meise, 2000). Related flatfishes, dab (*Pleuronectes limanda*) and plaice (*P. platessa*), as well as herring, cod (*Gadus callarius*), bib (*Trisopterus luscus*) and goby (*Pomatoschistus minutus*) also feed heavily on *E. affinis* (Scott, 1902; Hardy, 1924; Hostens and Mees, 1999). Further, preference for *E. affinis* over *Acartia* spp. has been noted for herring in the Baltic Sea (Sandstrom, 1980; Hansson et al., 1990; Rudstam et al., 1992).

Eurytemora affinis and *A. hudsonica* collected in the Navesink River were similar in size. Therefore, it is unlikely that prey size contributed to the preference for *E. affinis* over *A. hudsonica*. However, winter flounder diets primarily contained *E. affinis* in the larger size classes (0.20–0.25 and > 0.25 mm CW), suggesting size selectivity on the preferred species. Larger prey also became more important in diets as fish size increased, a feeding behavior observed previously in young winter flounder (Pearcy, 1962; Richards, 1963; Mulkana, 1966; Armstrong, 1995) and other fish species (Ghan and Sprules, 1993).

More female *E. affinis* than males were observed in the stomachs of the larger (> 19 mm TL) newly settled winter flounder. It is unclear, however, if selection was based solely on gender because females were characteristically larger than males (0.32 vs. 0.24 mm CW) during our study and newly settled fish preferred the largest prey. Yet, the consumption of female *E. affinis* could be advantageous: they are egg-bearing and considered more energetically valuable than the males (Castonguay and FitzGerald, 1990). Preference for female *E. affinis* also has been exhibited by Baltic herring (*Clupea harengus*) (Sandstrom, 1980) and three species of stickleback (*Gasterosteus aculeatus*, *G. wheatlandi*, and *Pungitius pungitius*) (Castonguay and FitzGerald, 1990). Sandstrom (1980) suggested that egg sacs increased the visibility and slowed the escape of females.

Acartia hudsonica was consumed readily by newly settled winter flounder in our laboratory monocultures. Therefore, the almost complete absence of this species from the stomachs of our field caught fish is counterintuitive. *Acartia hudsonica* should have been as accessible to newly settled winter flounder as *E. affinis*. Vertically, *A. hudsonica*

and *E. affinis* are more epibenthic than pelagic during daylight hours (Bollens and Frost, 1989; Castel and Veiga, 1990), when demersal newly settled winter flounder feed (MacPhee, 1978). Moreover, both species were observed just off bottom in our laboratory experiments. In the field, however, fine-scale differences in the distributions of the two species, undetected by our sampling methods, might have made *A. hudsonica* less available to young winter flounder than *E. affinis*. Monospecific swarms of both species have been observed in coastal and estuarine waters (Ueda et al., 1983; Tanaka, 1985; Heckman, 1986; Castonguay and FitzGerald, 1990). Yet, because both species were ubiquitous throughout the river during our surveys, it is unlikely that swarms of *A. hudsonica* were not encountered by the newly settled winter flounder.

Plasticity in vertical migratory behavior might allow *A. hudsonica* to avoid predation by newly settled winter flounder. Bollens et al. (1994) found that planktivorous predators induced *A. hudsonica* to adopt an epibenthic position during daylight. The reverse response, migration into the water column sufficiently high to evade the winter flounder, might be elicited from *A. hudsonica* in the presence of these demersal predators. We did not observe this behavior during our laboratory experiments. If it occurred in the field, the avoidance mechanism would have to be highly sophisticated to cause the near exclusion of *A. hudsonica* from the diets of young winter flounder.

Our research suggests that prey activity influenced prey selection by newly settled winter flounder. Adult winter flounder (Macdonald, 1983; Carlson et al., 1997) and other fish species (Zaret, 1980; Sullivan et al., 1983; Buskey et al., 1993; Pepin and Penney, 1997) are attracted to the most active prey. During our laboratory experiments, *E. affinis* may have been more visible to predators as a result of its erratic movements, than *A. hudsonica* which swam more rhythmically. Rudstam et al. (1992) attributed selection for *E. affinis* over *Acartia* spp. by herring to the higher activity level of *E. affinis*.

Also, differences in pigmentation and morphology might have attracted newly settled winter flounder to *E. affinis*. *Eurytemora affinis* appeared darker than *A. hudsonica* during our laboratory observations and the two species are easily differentiated. *Eurytemora affinis* has antennules with short setae, an oval head and elongate caudal rami, while *A. hudsonica* has long setae on the antennules, a 'coffin-shaped' head and short caudal rami. The body is oblong in both species. Zaret (1980) observed that fish could be highly discriminatory when distinguishing between prey items with similar gross morphologies. Thus, newly settled winter flounder could have selected *E. affinis* because a characteristic physical attribute made it more conspicuous than *A. hudsonica*.

Our laboratory experiments found that when newly settled winter flounder were fed either *E. affinis* or *A. hudsonica* (100% treatments), they were much less successful capturing the former than the latter (35 vs. 62% successful attacks), although an equal number of the prey species was consumed. A large number of the unsuccessful attacks on *E. affinis* might have been caused by its faster escape speed. Viitasalo and Rautio (1998) reported that *E. affinis* had a quicker escape speed than *Acartia* spp. and *E. affinis* was also more difficult for us to capture by pipette than *A. hudsonica*. Fast escape speeds are considered advantageous for predator evasion (Viitasalo and Rautio, 1998; Fields and Yen, 1997). However, our results suggest that this defense mechanism was ineffectual when *E. affinis* was preyed upon by newly settled winter flounder: *E. affinis* was just repeatedly attacked until capture. Subsequently, there was no difference in the number of *E. affinis* and *A. hudsonica* consumed during the 100% treatments.

Some of the most noteworthy results of our laboratory work were that newly settled winter flounder actively selected *E. affinis* over *A. hudsonica* when offered a choice (50% treatments), even though it was more difficult to capture. One would expect that the most easily captured prey would be preferred because pursuit is energetically expensive. It is unknown if *E. affinis* is nutritionally more beneficial than *A. hudsonica*, providing caloric compensation once consumed. Laboratory experiments might resolve that question. Based on our observations, however, the selective feeding behavior exhibited by young winter flounder during the 50% treatments most likely occurred because *E. affinis* was detected more easily than *A. hudsonica*.

Our research emphasizes the need for detailed information on the feeding behavior of young-of-the-year fish. In the Navesink River, NJ, *E. affinis* and *A. hudsonica* co-occur spatially and temporally with newly settled winter flounder and appear equitable prey. For newly settled winter flounder, however, behavioral and/or morphological attributes of *E. affinis* make it the prey of choice.

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References

Able, K.W., Fahay, M.P., 1998. The First Year in the Life of Estuarine Fishes in the Middle Atlantic Bight. Rutgers University Press, New Jersey.

Armstrong, M.P., 1995. A comparative study of the ecology of smooth flounder, *Pleuronectes putnami*, and winter flounder, *Pleuronectes americanus*, from Great Bay Estuary, New Hampshire. PhD dissertation, University of New Hampshire, Durham, 135 pp.

Blaxter, J.H.S., 1969. Experimental rearing of pilchard larvae, *Sardina pilchardus*. J. Mar. Biol. Assoc. UK 49, 557–575.

Bollens, S.M., Frost, B.W., 1989. Predator-induced diel vertical migration in a planktonic copepod. J. Plankton Res. 11, 1047–1065.

Bollens, S.M., Frost, B.W., Cordell, J.R., 1994. Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. J. Plankton Res. 16, 555–564.

Buskey, E.J., Coulter, C., Strom, S., 1993. Locomotory patterns of microzooplankton: potential effects on food selectivity of larval fish. Bull. Mar. Sci. 53, 29–43.

Carlson, J.K., Randall, T.A., Mroczka, M.E., 1997. Feeding habits of winter flounder (*Pleuronectes americanus*) in a habitat exposed to anthropogenic disturbance. J. Northwest Atl. Fish. Sci. 21, 65–73.

Castel, J., Veiga, J., 1990. Distribution and retention of the copepod *Eurytemora affinis hirundoides* in a turbid estuary. Mar. Biol. 107, 119–128.

Castonguay, M., FitzGerald, G.J., 1990. The ecology of the calanoid copepod *Eurytemora affinis* in salt marsh tide pools. Hydrobiologia 202, 125–133.

Chant, R.J., Stoner, A.W., 2000. Particle trapping in a stratified flood-dominated estuary. In review.

Checkley, Jr. D.M., 1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Mar. Ecol. Prog. Ser. 9, 245–253.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Cronin, L.E., Daiber, J.C., Hulbert, E.M., 1962. Quantitative seasonal aspects of zooplankton in the Delaware River Estuary. Chesapeake Sci. 3, 63–93.

Deevey, G.B., 1956. Oceanography of Long Island Sound, 1952–1954. V. Zooplankton. Bull. Bingham Oceanogr. Collect. Yale Univ. 15, 113–155.

Fields, D.M., Yen, J., 1997. The escape behaviour of marine copepods in response to a quantifiable fluid mechanical disturbance. J. Plankton Res. 19, 1289–1304.

Ghan, D., Sprules, W.G., 1993. Diet, prey selection, and growth of larval and juvenile burbot *Lota lota* (L.). J. Fish Biol. 42, 47–64.

Hansson, S., Larsson, U., Johansson, S., 1990. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J. Plankton Res. 12, 1099–1116.

Hardy, A.C., 1924. The herring in relation to its animate environment. Part 1. The food and feeding habits of the herring with special reference to the east coast of England. Fish. Invest. Ser. II 7 (3), 1–53.

Heckman, C.W., 1986. The anadromous migration of a calanoid copepod, *Eurytemora affinis* (Poppe, 1880) in the Elbe estuary. Crustaceana 50, 176–181.

Hostens, K., Mees, J., 1999. The mysid-feeding guild of demersal fishes in the brackish zone of the Westerschelde estuary. J. Fish Biol. 55, 704–719.

Jeffries, H.P., 1959. The plankton biology of Raritan Bay. PhD thesis, Rutgers University, New Brunswick, 180 pp.

Kimmerer, W.J., McKinnon, A.D., 1989. Zooplankton in a marine bay. III. Evidence for influence of vertebrate predation on distributions of two common copepods. Mar. Ecol. Prog. Ser. 53, 21–35.

Lee, W.Y., McAlice, B.J., 1979. Sampling variability of marine zooplankton in a tidal estuary. Estuar. Coast. Mar. Sci. 8, 565–582.

Macdonald, J.S., 1983. Laboratory observations of feeding behavior of the ocean pout (*Macrozoarces americanus*) and winter flounder (*Pseudopleuronectes americanus*) with reference to niche overlap of natural populations. Can. J. Zool. 61, 539–546.

MacPhee, G.K. (Ed.), 1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). NOAA (National Oceanographic Atmospheric Administration) Technical Report. NMFS (National Marine Fisheries Service), Circular 414.

Monteleone, D.M., Peterson, W.T., 1986. Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. Mar. Ecol. Prog. Ser. 30, 133–143.

Mulkana, M.S., 1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2, 97–167.

Pearcy, W.G., 1962. Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus* (Walbaum). Bull. Bingham Oceanogr. Collect. Yale Univ. 18, 1–78.

Pepin, P., Penney, R.W., 1997. Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? J. Fish Biol. 51 (Suppl. A), 84–100.

Peterson, W.T., Ausubel, S.J., 1984. Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar. Ecol. Prog. Ser. 17, 65–75.

Phelan, B.A., Goldberg, R., Bejda, A.J., Pereira, J., Hagan, S., Clark, P., Studholme, A.L., Calabrese, A., Able, K.W., 2000. Estuarine and habitat-related differences in growth rates of young-of-the-year winter flounder (*Pseudopleuronectes americanus)* and tautog (*Tautoga onitis*) in three northeastern US estuaries. J. Exp. Mar. Biol. Ecol. 247, 1–28.

Richards, S.W., 1963. The demersal fish population of Long Island Sound. II. Food of the juveniles from a sand-shell locality (Station 1). Bull. Bingham Oceanogr. Collect. Yale Univ. 18, 32–72.

Rudstam, L.G., Hansson, S., Johansson, S., Larsson, U., 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Prog. Ser. 80, 159–173.

Sage, L.E., Herman, S.S., 1972. Zooplankton of the Sandy Hook Bay area, NJ. Chesapeake Sci. 13, 29–39.

Sandstrom, O., 1980. Selective feeding by Baltic herring. Hydrobiologia 69, 199–207.

Scott, T., 1902. Observations on the food of fishes. Rep. Fish. Board Scot. 1902, 486–538.

Shaheen, P.A., Steimle, F.W., 1995. Trends in copepod communities in the Navesink and Shrewsbury Rivers, New Jersey: 1962–1992. Estuaries 18, 250–254.

Stehlik, L.L., Meise, C.J., 2000. Diet of winter flounder in a New Jersey estuary: ontogenetic change and spatial variation. Estuaries 23, 381–391.

Stepien, J.C., Malone, T.C., Chervin, M.B., 1981. Copepod communities in the estuary and coastal plume of the Hudson River. Estuar. Coast. Shelf Sci. 13, 185–195.

Stoecker, D.K., Govoni, J.J., 1984. Food selection by young larval gulf menhaden (*Brevoortia patronus*). Mar. Biol. 80, 299–306.

Stoner, A.W., Bejda, A.J., Manderson, J.P., Phelan, B.A., Stehlik, L.L., Pessutti, J.P., 1999. Behavior of winter flounder, *Pseudopleuronectes americanus*, during the reproductive season: Laboratory and field observations of the spawning, feeding, and locomotion. Fish. Bull. US 97, 999–1016.

Stoner, A.W., Manderson, J.P., Pessutti, J.P., 2000. Spatially-explicit analysis of habitat for juvenile winter flounder (*Pseudopleuronectes americanus*): combining generalized additive models and geographic information systems. In press.

Sullivan, B.K., Buskey, E., Miller, D.C., Ritacco, P.J., 1983. Effects of copper and cadmium on growth, swimming and predatory avoidance in *Eurytemora affinis* (Copepoda). Mar. Biol. 77, 299–306.

Tanaka, M., 1985. Factors affecting the inshore migration of pelagic larval and demersal juvenile red sea bream *Pagrus major* to a nursery ground. Trans. Am. Fish. Soc. 114, 471–477.

Ueda, H., Kuwahara, A., Tanaka, M., Azeta, M., 1983. Underwater observations on copepod swarms in temperate and subtropical waters. Mar. Ecol. Prog. Ser. 11, 165–171.

Viitasalo, M., Rautio, M., 1998. Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. Mar. Ecol. Prog. Ser. 174, 77–87.

Yamazi, I., 1966. Zooplankton communities of the Navesink and Shrewsbury Rivers and Sandy Hook Bay, New Jersey. Bur. Sport Fish. Wildl. Tech. Pap. 2, 1–44.

Zaret, T.M., 1980. The effect of prey motion on planktivore choice. In: Kerfoot, W.C. (Ed.), Evolution and Ecology of Zooplankton Communities. University Press of New England, Hanover, NH, pp. 594–603.